

## 2 THE EFFECTS OF INTERNAL AND EXTERNAL CONTROL ON THE NORTHERN BENGUELA ECOSYSTEM

*Johanna J. Heymans\**

### *Abstract*

Internal and external control of the northern Benguela ecosystem over the past 30 years was examined using the steady-state Ecopath model of the ecosystem, created for the 1970s and simulating to the present. The effect of an external factor such as fishing was combined with the internal “wasp-waist” control of the ecosystem by forage species such as anchovy and sardine (i.e. top-down control on their prey and bottom-up control on their predators). The effect of including these external and internal control factors increased the fit of the model to the observed data by 50%. Six primary production forcing anomalies were subsequently predicted by Ecosim, three with “wasp-waist” forcing included and three without. The three scenarios with internal control increased the fit of the model to 65%. When no internal control was included, the goodness of fit only increased marginally. The primary production forcing functions predicted by Ecosim in these six scenarios were then correlated to environmental variables such as summer and winter sea surface temperature as well as pseudo-wind stress anomalies. Significant correlations were obtained for summer sea surface temperature and pseudo-wind stress anomalies when “wasp-waist” control was invoked.

### INTRODUCTION

Upwelling ecosystems, by their very nature, are affected by external forces such as environmental variation and fishing. The northern Benguela ecosystem is no exception. The effects of these external forces on the northern Benguela ecosystem have been described by various authors, *viz.* Boyer *et al.*

---

\* The author would like to thank Chris Bartholomae, Astrid Jarre, Claude Roy, Lynne Shannon, Nico Willemse, and the Ministry of Fisheries and Marine Resources for the data and models provided for this work. Thank you also to Villy Christensen, Robyn Forrest, Lynne Shannon and to two anonymous reviewers for their assistance and comments.

(2001); Boyer and Hampton (2001); Cole (1999); Cole and Villacastin (2000); Kreiner *et al.* (2000) and Reid *et al.* (2000).

The environmental forces driving upwelling in the northern Benguela ecosystem are persistent southerly winds, which impact sea surface temperature (SST), nutrient supply and primary productivity (Shannon *et al.*, 1990). Primary production, in turn, drives fish production and Jarre-Teichmann and Christensen (1998) suggest that 15-30% of total primary production is needed to sustain major pelagic fish communities in upwelling areas. Thus, these external forces also impact the important forage species in the northern Benguela ecosystem.

Kreiner *et al.* (2000) showed that wind anomalies are a good predictor of sardine spawner biomass and recruitment, while Reid *et al.* (2000) suggested that sardine play a role in controlling primary productivity and during periods of low sardine abundance, the result could be eutrophication due to under-utilisation of phytoplankton (Boyer *et al.*, 2001). In addition, Cole (1999) found that sea surface temperature usually acts as a good proxy for recruitment success in both anchovy and sardine, although for one year in his study (1987), both anchovy and sardine recruitment was high, probably due to the good oceanographic conditions for onshore retention of eggs and high nutrient enrichment (Cole, 1999).

Internal forces, such as predator-prey interactions, competition, etc., also affect ecosystems. The internal control of predators and prey in an ecosystem could be top-down (i.e. predators control their prey), bottom-up (i.e. prey control the abundance of predators) or a mixture of those. Cury *et al.* (2000) suggest that in the Benguela ecosystem there is limited evidence of top-down control of forage fish by predator populations, with more substantial bottom-up control of predators by forage fish. They postulate that one might expect to observe strong interactions between primary production and pelagic fish, mediated through zooplankton, by means of "wasp-waist" control. Under "wasp-waist" control, zooplankton is highly vulnerable to predation by small pelagic fish such as anchovy, sardine, etc. and therefore, competition for zooplankton prey is reduced when fishing is increased (Cury *et al.*, 2000). Thus, in the northern Benguela ecosystem, both zooplankton and top predators are controlled by small pelagic fish such as anchovy, sardine, etc., thus both the top and the bottom of the ecosystem are being controlled by the middle trophic level, and removing large quantities of species from the system, as was done in the 1970s and 1980s, would have severe effects on the ecosystem.

External control of the Benguela ecosystem includes both fishing and environmental forcing. The effects of fishing and internal forcing have been studied in the southern Benguela system by Cury *et al.* (2000) and Shannon *et al.* (2000), while the effects of fishing and internal control in the northern

Benguela ecosystem have been attempted by J.-P. Roux (unpublished work). However, the combined effect of the internal forcing of “wasp-waist” control and *both* anthropogenic and natural external forcing (i.e. fishing and environmental variation) on the northern Benguela ecosystem has not been attempted. This paper therefore examines the effects of environmental forcing functions, fish catches and “wasp-waist” control of forage fish on the northern Benguela ecosystem to see if the combined effect of these factors could explain the variation in the ecosystem over time.

## THE ECOSYSTEM

The northern Benguela ecosystem (Figure 1) is bound to the north by the Angolan front at approximately 15°S (Shannon *et al.*, 1987; Lutjeharms and Meeuwis, 1987) and to the south by the Lüderitz upwelling cell, with the official limit set close to the South African-Namibian border at 29°S (Brown *et al.*, 1991). There are four main upwelling cells in the northern Benguela: the Kunene cell, Namibia cell (or Cape Frio cell, Figure 1), Walvis Bay cell and Lüderitz cell (Lutjeharms and Meeuwis, 1987). The temperatures of all upwelled waters south of the Angola Front vary between 10 and 19°C.

Upwelling in the northern Benguela is wind driven, with the climatic forcing being produced mainly by the South-East Atlantic High Pressure anticyclone that causes persistent equatorward winds north of 32°S (Estrada and Marrase, 1987). The seaward extent of the major wind-induced upwelling cells ranges from nearly 150 km at the Namibia cell (19°S) to close to 300 km at the Lüderitz cell (27°S) (Lutjeharms and Meeuwis, 1987). The wind stress for all upwelling cells is from the south-east and the climatic Ekman drift is suitable for year-long upwelling along the whole coast (Lutjeharms and Meeuwis, 1987).

There are five major species of commercial importance in the northern Benguela ecosystem: Cape anchovy (*Engraulis capensis*), sardine (*Sardinops sagax*), horse mackerel (*Trachurus capensis*) and hake (*Merluccius capensis* and *M. paradoxus*). The two species of hake are usually reported in catch statistics as one group. The total cumulative catch of anchovy, sardine, horse mackerel and hake since the Second World War is approximately 4, 15, 12, and 12 million tonnes respectively (Boyer *et al.*, 2000).

Anchovy was important in the ecosystem and the fishery until recently, but since the mid 1990s very little has been caught, and surveys in the late 1990s indicated that their biomass is very low (Boyer and Hampton, 2001). Shackleton (1987) has examined the interaction between anchovy and sardine (the two main forage species) over the previous 100 years by looking at the fossil fish scales in a core off Walvis Bay. She found that sardine and

anchovy seemed to decline over two 20-year periods, with sardine recovering ahead of anchovy. Subsequent to the recovery, the two stocks alternated in dominance, with the combined stock size remaining constant over those periods (Shackleton, 1987). Overall, the scale analysis showed that the stocks decreased by a factor of 8 over the century, and that the community was always sardine dominated (Shackleton, 1987).

The estimates of sardine biomass and catch show a clear reduction since the start of the fishery. Excessive fishing and recruitment failure seems to have been the reason for the stock collapse in the 1960s and 1970s (Cram, 1981 in Fossen *et al.*, 2001). Fishing mortality increased since the mid 1970s and was an important cause of mortality until 1990 (Thomas, 1986 in Fossen *et al.*, 2001). The fishing mortality of northern Benguela sardine was much

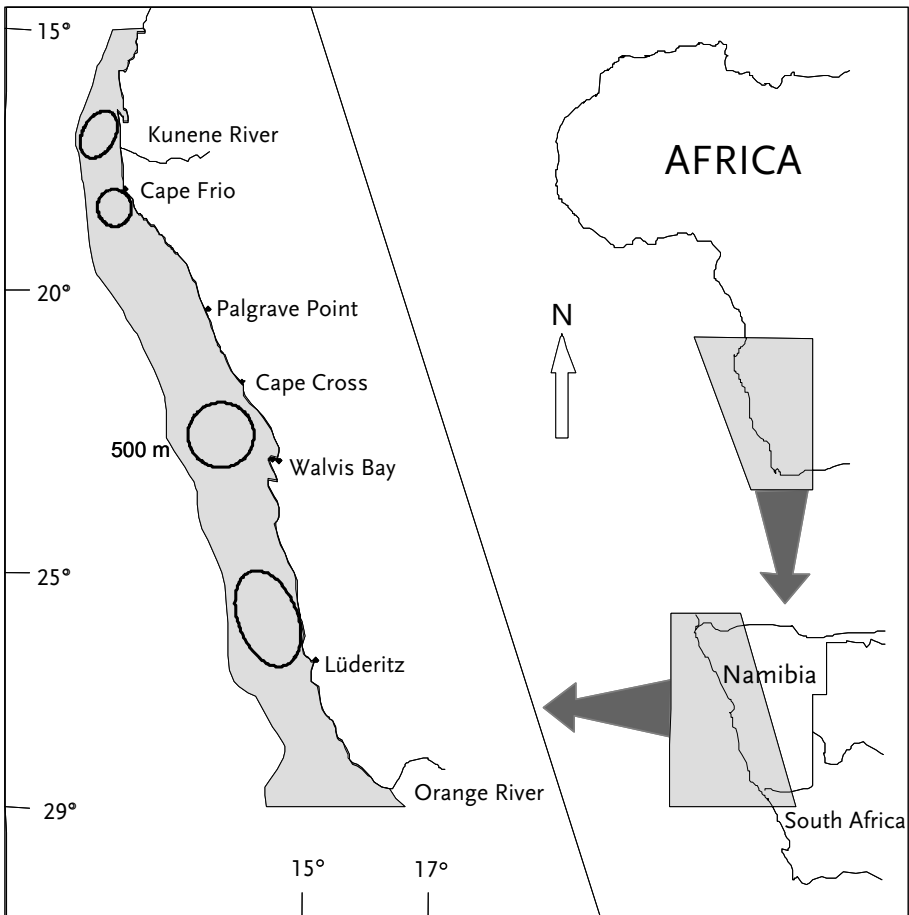


Figure 1. Schematic representation of the Northern Benguela ecosystem (from Heymans, 1997) showing the 500 m depth contour and upwelling cells (redrawn from Lutjeharms and Meeuwis, 1987).

lower in the 1990s (Fossen *et al.*, 2001), but by the end of that decade the sardine stock had still not recovered. According to Fossen *et al.* (2001) the fishing pressure during the past four decades has been at least one of the reasons for the increased total mortality. High fishing mortality contributed to the stock collapse and low abundance during the 1970s and 1980s, but current mortality rates seem to be controlled mainly by other factors, such as a change in growth rate and/or higher predation mortality (Fossen *et al.*, 2001). The higher predation mortality is probably due to their low biomass causing higher vulnerability to predators (Fossen *et al.*, 2001).

Hakes are the most commercially important demersal fish in the northern Benguela system (Boyer *et al.*, 2000). Two species of hake are caught along the Namibian coast – deep-water hake (*Merluccius paradoxus*) and shallow-water Cape hake (*M. capensis*). In Namibia, shallow-water hake is more abundant than the deep-water species, but the biomass of deep-water hake has increased since 1990 (Burmeister, 2001). Cape hake is mainly distributed off central and northern Namibia, while deep-water hake extends from the southern Benguela (Boyer *et al.*, 2000). There are indications that adult Cape hake feed on juvenile deep-water hake (Boyer *et al.*, 2000).

Horse mackerel is the only mesopelagic species that is currently fished in the northern Benguela (Boyer *et al.*, 2000). Cape horse mackerel (*Trachurus capensis*) have a wide distribution, from Lüderitz to Angola and from the surf zone to beyond the shelf break, but their highest concentrations are between 17°S and 22°S (Boyer *et al.*, 2000). Cunene horse mackerel (*Trachurus trechae*), in contrast, occurs in northern Namibia and southern Angola and overlaps with Cape horse mackerel at the southern end of their range (Boyer *et al.*, 2000).

## METHODOLOGY

Heymans *et al.* (2004) compared the three Ecopath models of the northern Benguela ecosystem constructed by Jarre-Teichmann (1998); Jarre-Teichmann and Christensen (1998); Shannon and Jarre-Teichmann (1999) and Heymans and Baird (2000). The earliest of these models (1971-1977), constructed by Jarre-Teichmann (1998); Jarre-Teichmann and Christensen (1998) and adapted in Heymans *et al.* (2004), was subjected to time series fitting here, using Ecosim in the Ecopath with Ecosim (*EwE* version 5 Beta) suite. The Ecopath with Ecosim methodology, functions, equations, etc. are well explained in Christensen *et al.* (2000); Christensen and Walters (2004); Walters *et al.* (1997) and Walters *et al.* (2000), however, a brief description is given here.

Ecopath is a mass balance approach that creates a static model of the ecosystem and uses two master equations to parameterise the model; one for the energy balance of each group (Eq. 1) and the other to depict the production term (Eq. 2 and 3) (Christensen and Walters, 2004). The energy balance for each group is calculated *sensu* Winberg (1956), who defined consumption as the sum of somatic and gonadal growth, metabolic costs and waste product (Christensen and Walters, 2004). Consumption is calculated with the formula:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (1)$$

The total production rate  $P_i$  for each group  $i$  is given by:

$$P_i = Y_i + M2_i \cdot B_i + E_i + BA_i + M0_i \cdot B_i \quad (2)$$

where  $Y_i$  is the total fishery catch rate of  $i$ ,  $M2_i$  is the instantaneous predation rate for group  $i$ ,  $E_i$  the net migration rate (emigration  $\cdot$  immigration),  $BA_i$  is the biomass accumulation rate for  $i$ , while  $M0_i$  is the 'other mortality' rate for  $i$ .  $P_i$  is calculated as the product of  $B_i$ , the biomass of  $i$  and  $(P/B)_i$ , the production/biomass ratio for  $i$ . The  $(P/B)_i$  rate under most conditions corresponds to the total mortality rate,  $Z$  (Allen, 1971), commonly estimated as part of fishery stock assessments (Christensen and Walters, 2004). This can be re-written as:

$$P_i = \frac{Y_i + E_i + BA_i + \sum_j Q_j \cdot DC_{ji}}{EE_i} \quad (3)$$

where  $EE_i$ , the ecotrophic efficiency of group  $i$ , describes the proportion of the production that is utilised in the system as described,  $Q_j$  is the total consumption rate for group  $j$ , and  $DC_{ji}$  is the fraction of predator  $j$ 's diet contributed by prey  $i$ .  $Q_j$  is calculated as the product of  $B_j$ , the biomass of group  $j$  and  $(Q/B)_j$ , the consumption/biomass ratio for group  $j$  (Christensen and Walters, 2004).

Ecosim uses a set of differential equations to calculate the changes in biomass of each group over time, by using the harvest rates as well as external forcing functions imposed on the ecosystem (Christensen *et al.*, 2000).

The equations are derived from the Ecopath master (Eq. 2), and take the form:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M0_i + F_i + e_i) \cdot B_i \quad (4)$$

where  $dB_i/dt$  represents the growth rate during the time interval  $dt$  of group  $i$  in terms of its biomass,  $B_i$ ,  $g_i$  is the net growth efficiency,  $M0_i$  the non-predation ('other') natural mortality rate,  $F_i$  is fishing mortality rate,  $e_i$  is emigration rate,  $I_i$  is immigration rate (assumed constant over time, and hence independent of events in the ecosystem modelled), and  $e_i \cdot B_i - I_i$  is the net migration rate of Eq. 2 (Christensen and Walters, 2004). The two summations estimate consumption rates, the first calculating the total consumption by group  $i$ , and the second the predation by all predators on the same group  $i$ . The consumption rates,  $Q_{ij}$ , are calculated based on the 'foraging arena' concept, where  $B_i$ 's are divided into vulnerable and invulnerable components *sensu* Walters *et al.* (1997). The transfer rate ( $v_{ij}$ ) between the vulnerable and invulnerable components determines if control is top down (i.e. Lotka–Volterra), bottom up (i.e. donor-driven), or of an intermediate type (Christensen and Walters, 2004). Top-down versus bottom-up control is a continuum in the model, where low  $v$ 's implies bottom-up and high  $v$ 's top-down control. Consumption at each timestep is calculated by:

$$Q_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot M_{ij} / D_j}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot B_j \cdot S_{ij} \cdot T_j / D_j} \quad (5)$$

where  $a_{ij}$  is the rate of effective search for  $i$  by  $j$ ,  $T_i$  represents prey relative feeding time,  $T_j$  the predator relative feeding time,  $S_{ij}$  the user-defined seasonal or long term forcing effects,  $M_{ij}$  the mediation forcing effects, and  $D_j$  represents effects of handling time as a limit to consumption rate (see Walters *et al.*, 1997, 2000 and Christensen and Walters, 2004 for further information on these algorithms).

### Time series data

Catch estimates for all species in the northern Benguela ecosystem were obtained from Willemse (2002) and Willemse and Pauly (*this volume*). The biomass estimates for each group were obtained from various sources and are explained below. The biomass estimates of anchovy were obtained from the Namibian Ministry of Fisheries and Marine Resources (see Heymans, 1997) for the time period 1990–1995. No estimates of biomass were available for anchovy prior to 1990 and subsequent to 1995 no surveys for anchovy were done, due to the low biomass (Boyer *et al.*, 2001). The catch and biomass estimates for anchovy are shown in Figure 2.

Biomass estimates of sardine from 1990 to 2000 were obtained from Fig. 4 in Boyer *et al.* (2001). Biomass estimates for 1971 to 1989 were obtained from Thomas (1986), and correlate well with the biomass trajectory given in Fossen *et al.* (2001). See Figure 3 for the catch and biomass estimates of sardine in the northern Benguela ecosystem.

Biomass estimates of hake were not readily available prior to 1990, but Butterworth and Geromont (2001) gives CPUE for ICSEAF Divisions 1.3+1.4 and 1.5 for 1965-1988, and from General Linear Modelling for 1991-1996 (Figure 4). The summer and winter biomass estimates made by the Research Vessel Dr. Fridtjof Nansen for 1990 to 1997 are also given by Butterworth and Geromont (2001) (see Figure 4), and Burmeister (2001) gives depth-stratified biomass estimates for both species of hake from 1990 to 1999 (Figure 5). The

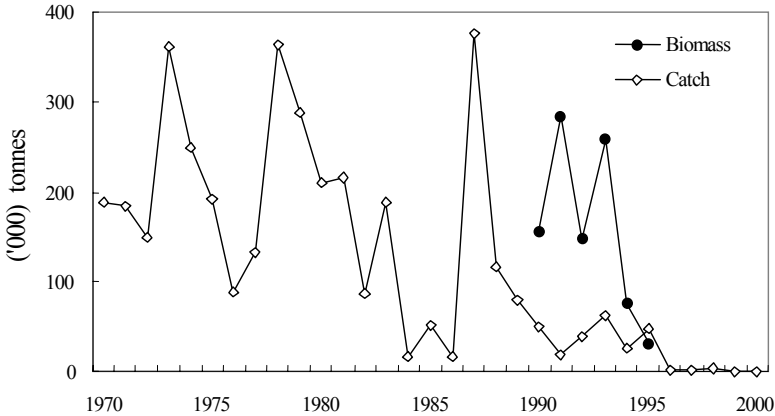


Figure 2. Catch and biomass estimates (tonnes) of anchovy from 1970 to 2000 in the northern Benguela ecosystem. Biomass estimates obtained from the Ministry of Fisheries and Marine Resources and catches from Willemsse and Pauly (*this volume*).

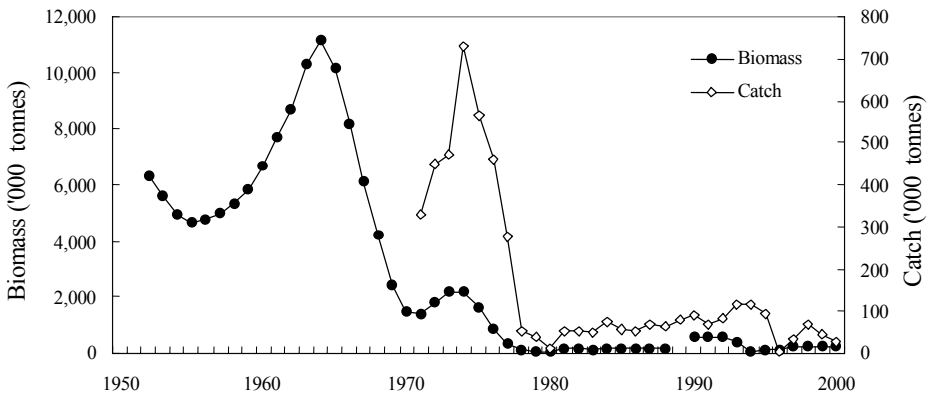


Figure 3. Catch and biomass estimates of sardine from 1951 to 2000 in the northern Benguela ecosystem. Biomass estimates obtained from Willemsse and Pauly (*this volume*) and Boyer *et al.* (2001) and catches from Willemsse and Pauly (*this volume*).



biomass estimates obtained from Burmeister (2001) and the CPUE for ICSEAF Divisions 1.3+1.4 were used to compare the biomass estimates for hake (Butterworth and Geromont, 2001). The two species of hake are not specified in the landings and therefore they were combined into one stock. See Figure 5 for catch and biomass of hake.

Time series data for horse mackerel were not as easy to obtain as for hake and sardine, even though horse mackerel has a large biomass at present in the system. Biomass estimates were not available prior to 1989, but estimates from 1989 to 1998 were obtained from acoustic surveys (Vaske and Klingel-

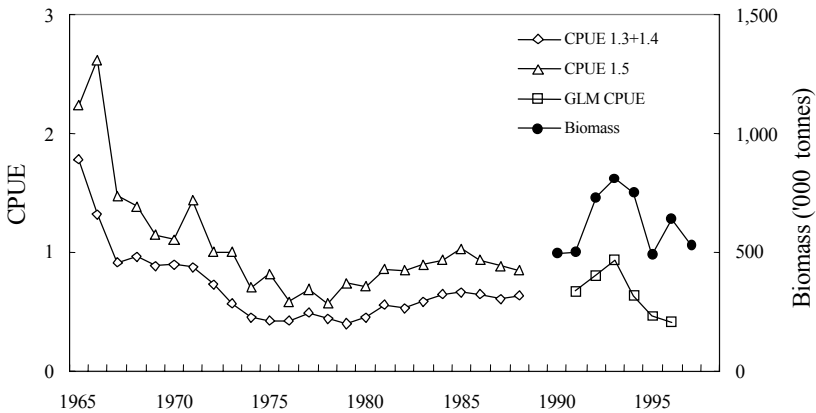


Figure 4. CPUE estimates and biomass estimates of hake stocks in the northern Benguela ecosystem for 1965 to 1997 obtained from Butterworth and Geromont (2001).

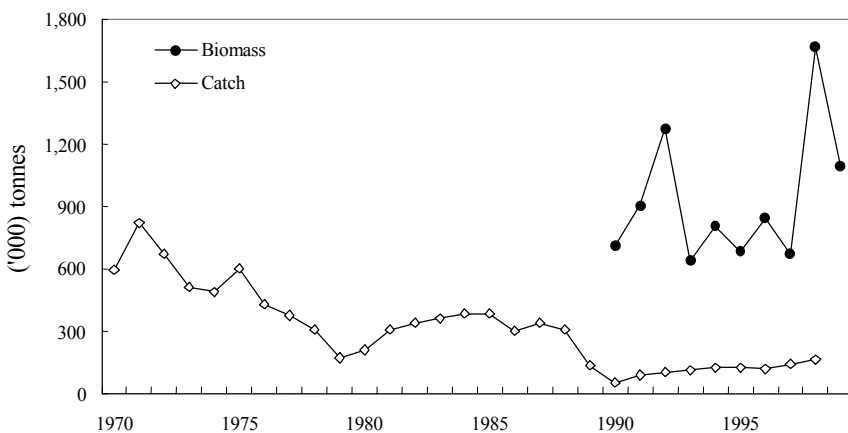


Figure 5. Catch and biomass estimates of hake from 1971 to 2000 in the northern Benguela ecosystem. Biomass estimates obtained from Burmeister (2001) and catches from Willemse and Pauly (*this volume*).

hoeffer (2001) and Nico Willemse (*pers. comm.*). See Figure 6 for catch and biomass of horse mackerel.

### Time series fitting

The time series data described above, for catch and biomass of the four most important groups (anchovy, sardine, hake and horse mackerel) were used to calculate harvest rates (catch/biomass). These harvest rates were used to drive the 1970s model to the present time period by changing the biomass of the different groups with the changes in harvest rate. Ecosim estimates a goodness-of-fit measure to estimate the variance between the predicted and observed parameters. The goodness-of-fit measure is a weighted sum of squares (SS) deviation of log biomasses from log predicted biomasses (Christensen and Walters, 2004).

### Vulnerability changes

In Ecosim it is assumed that prey are split into two groups in accordance with the “foraging arena theory”: those that come out to feed and are therefore vulnerable to predation, and those that hide from predators but also don’t get to feed (Christensen and Walters, 2004). Predation rates are therefore limited by the flow of prey between vulnerable and invulnerable groups, and the more time a prey spends feeding, the higher is its vulnerability to predators (Walters *et al.*, 2000). This vulnerability is also dependent on the biomass of the predator with respect to its unfished biomass (Christensen

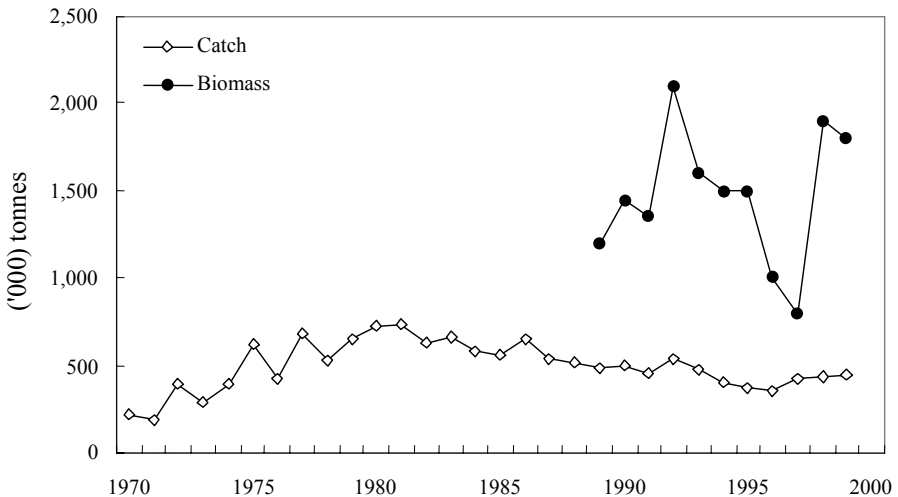


Figure 6. Catch and biomass estimates of horse mackerel from 1971 to 2000 in the northern Benguela ecosystem. Biomass estimates obtained from the Namibian Ministry of Fisheries and Marine Resources and catches from Willemse and Pauly (*this volume*).

and Walters, 2004). The vulnerabilities are scaled between 0 and 1, with 0 defining bottom-up flow control, 1 delineating top-down flow control and 0.3 serving as the default for mixed control (Christensen and Walters, 2004). It is consequently possible to test the two extremes of predator control, i.e. “top down” or “bottom up”, as well as the intermediate “wasp-waist” control by forage species (Christensen *et al.*, 2000). As a result of the work done by Shannon *et al.* (2000) and Cury *et al.* (2000) in the southern Benguela ecosystem, the vulnerabilities in this model were adapted to include the “wasp-waist” control of forage fish, *viz.* sardine and anchovy. “Wasp-waist” control by forage fish occurs when these fish exert top-down control on their prey and bottom-up control on their predators (Cury *et al.*, 2000; Shannon *et al.*, 2000). “Wasp-waist” control of sardine and anchovy on zooplankton and other prey were included by increasing the vulnerability of the prey to sardine and anchovy from the default of 0.3 to 0.6, and by decreasing vulnerability of sardine and anchovy to its predators to 0.1.

### Estimating primary production anomalies

The effects of the external forcing of environmental variables were inspected by first letting Ecosim derive forcing functions, or primary production anomalies, that would correlate best with the empirical time series data, and reduce the sum of squares of the output time series. Time series fitting was done by using a splicing value of five and by only fitting values from 1971 to 1999, excluding 2000. Six scenarios were tested, the first three with “wasp-waist” control and the final three without:

- “wasp-waist” control and forcing function on phytoplankton only;
- “wasp-waist” control and forcing function on phytoplankton and macrophytes;
- “wasp-waist” control and forcing function on phytoplankton and macrophytes, but with the weighting on hake CPUE reduced to 50%;
- no “wasp-waist” control, but with a forcing function on phytoplankton only;
- no “wasp-waist” control, but with a forcing function on phytoplankton and macrophytes;
- no “wasp-waist” control, but with a forcing function on phytoplankton and macrophytes, and with the weighting on hake CPUE reduced to 50%.

### Correlations with environmental variables

Average summer and winter sea surface temperature data for the area 24-26°S, 9-11°E were obtained for 1971-1995. The data were extracted by Claude Roy<sup>1</sup> from the COADS release laboratory dataset (Woodruff *et al.*, 1987) by

---

<sup>1</sup> Email: claude.roy@ird.fr

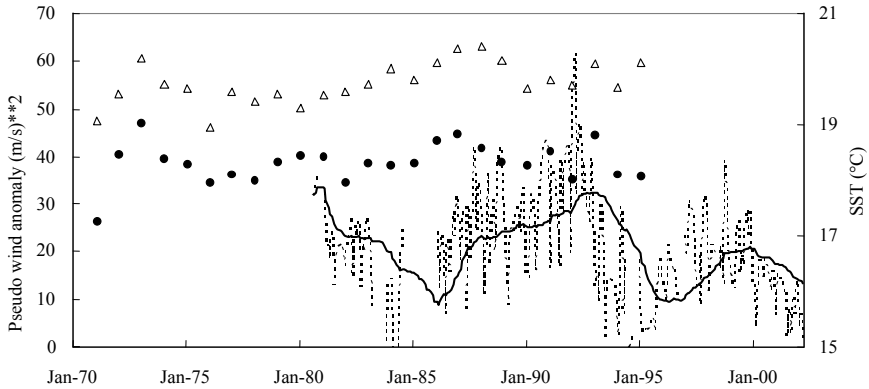


Figure 7. Environmental variables used for correlating to the primary production anomalies estimated by Ecosim. Triangles and dots are average summer and winter SST from 1971 to 1995 respectively. The dashed lines are the daily mean pseudo wind stress as the north-south wind speed in  $m.s.^{-1}$  and the solid black line is the three-year average trend-line of pseudo wind stress. Data obtained from Claude Roy (SST) and Ministry of Fisheries and Marine Resources (pseudo-wind stress anomalies).

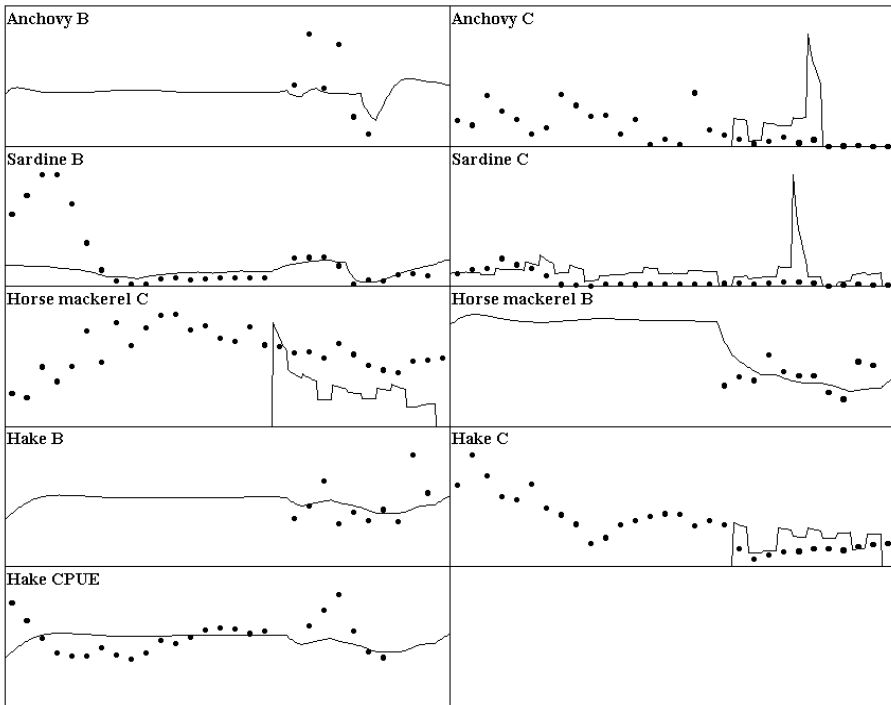


Figure 8. First run of the 1971-1977 model with time series data incorporated ( $SS = 216$ ). The x-axis represents the time series modelled (1971-2000) and the y-axis shows the relative change in the measured parameter, with C being catch, B being biomass and CPUE being catch per unit effort.

means of an updated version of the CODE software (Mendelssohn and Roy, 1996), and used by Roy in Shannon and Crawford (2003). Daily mean pseudo wind stress data (as the north-south wind speed in  $\text{m}\cdot\text{s}^{-1}$ ) for 1980-2002 were obtained from the Namibian Ministry of Fisheries and Marine Resources in Swakopmund (Chris Bartholomae<sup>2</sup>, *pers. comm.*). These data are shown in Figure 7.

The three-year average summer and winter sea surface temperature, as well as the three-year average pseudo wind stress, were then correlated to the three-year average forcing functions obtained for the six scenarios.

## RESULTS

### Time series fitting

The first run of the model excluded any internal forcing and only included the effects of the catch rate of the four groups discussed above. In this run, the sum of squares deviation was 216 (Table 1) and the results from this run are shown in Figure 8. In the second run of the model, “wasp-waist” control by sardine was included, which decreased the sum of squares from 216 to 146 (Table 1). In addition, including “wasp-waist” control of anchovy (0.6 for prey and 0.1 for predators) decreased the sums of squares marginally to 145.

### Environmental forcing

$EwE$  was used to derive forcing functions, or primary production anomalies, which would correlate best with the input data as a time series, and reduce the sums of squares of the output time series. Six scenarios were tested, three with “wasp-waist” control and three without. The resulting 3-year average of the six forcing functions are shown in Figure 9.

The sum of squares was reduced to 56 in Scenarios 1 and 2, and to 53 in Scenario 3. However, without “wasp-waist” control the sum of squares was not as low, being 133, 135 and 132 respectively for scenarios 4, 5 and 6 (Table 1). Thus, scenario 3, the estimated production anomaly on both phytoplankton and macrophytes with a reduced weighting on the CPUE of hake, reduced the sum of squares the most.

Ecosim calculates the probability distribution for the F statistic  $SS_{\text{reduced}}/SS_{\text{base}}$  by using the null hypothesis that there are no real productivity anomalies (Christensen *et al.*, 2000), i.e. that the emergent primary production anomalies obtained in scenarios 1-6 can be explained by chance alone. This is done by using a Monte Carlo simulation procedure to account for autocorrelation in the model residuals (Christensen *et al.*, 2000). The

---

<sup>2</sup> Email: cbartholomae@mfmr.gov.na

probability that the emergent primary production anomaly explained environmental effects by chance alone was lowest in scenarios 1, 2 and 3 ( $P < 0.001$ ), and highest in scenario 5 ( $P = 0.002$ ), with scenarios 4 and 6 being intermediate ( $P = 0.001$ ). However, Christensen *et al.* (2000) warns that even if there is a statistically significant reduction in sum of squares by using the search procedure, the estimated relative primary production values could still be misleading, and one can only postulate that “*assuming that primary production was in fact variable and that this did cause changes in relative abundance throughout the foodweb, then our best estimate of the historical pattern of variation is the one obtained by the fitting procedure*” (Christensen *et al.*, 2000).

### Comparison of predicted primary production anomaly and environmental variables

Two types of environmental factors that have been hypothesised to drive the northern Benguela ecosystem and that are tested here are SST (Cole, 1999) and wind anomalies (Kreiner *et al.*, 2000). The correlation between the three-year average summer and winter sea surface temperatures, three-year average pseudo wind stress and the three-year averages of the forcing functions

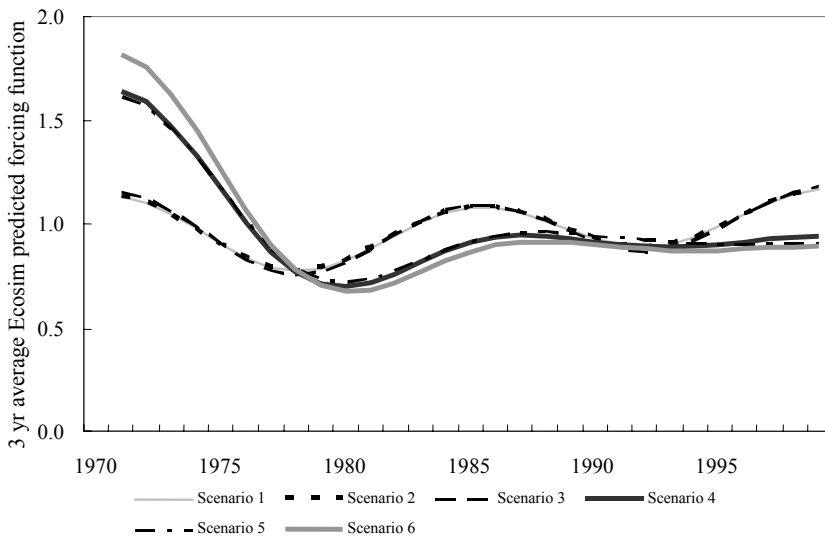


Figure 9. Three-year running average primary production anomaly predicted as a forcing function by Ecosim when using the time series data described in the text. Scenario 1 is a forcing function estimated only for phytoplankton, scenario 2 a forcing function for phytoplankton and macrophytes, and scenario 3 a forcing function for phytoplankton and macrophytes, but the weighting of hake CPUE was reduced to 50% in this scenario. Scenarios 4-6 are the same as scenarios 1-3 but the vulnerability settings were kept at 0.3, i.e. no “wasp-waist” control was imposed.

obtained from the six scenarios are shown in Figures 10-12. Correlation coefficients and significance are given in Table 1.

From the correlation coefficients in Table 1 and Figures 10-12 it was evident that the forcing functions estimated by Ecopath did not correlate well with winter SST, while there was a significant positive correlation with summer SST and a significant negative correlation with wind stress in scenarios 1-3. Scenarios 4, 5 and 6 (namely those that excluded “wasp-waist” control) did not show significant correlations with any of the environmental variables. The scenario that best correlated to summer SST was scenario 2, while scenario 1 correlated best to wind stress. The correlation with wind stress was significant at  $P = 0.01$  while the correlation to summer SST was only significant at  $P = 0.05$ .

Finally, plots of the best fit of the model to the data, for the predicted biomass and catch estimates using wasp-waist control and assuming a forcing function on both phytoplankton and macrophytes (i.e. scenario 2) are given in Figure 13.

Table 1. Sum of squares deviation of log biomasses from log predicted biomasses, as well as correlation coefficients ( $r$ ) and significance of correlations between environmental variables (average three-year averages of summer SST, winter SST and wind stress) and the six scenarios. Scenario 1 is a forcing function estimated only for phytoplankton, scenario 2 a forcing function for phytoplankton and macrophytes, and scenario 3 a forcing function for phytoplankton and macrophytes, but the weighting of hake CPUE was reduced to 50% in this scenario. Scenarios 4-6 are the same as scenarios 1-3 but the vulnerability settings were kept at 0.3, i.e. no “wasp-waist” control was imposed.

	Sum of Squares	Summer SST	Winter SST	Pseudo-wind stress
First run	216	-	-	-
“Wasp waist”	146	-	-	-
Scenario 1	56	0.470*	0.388	-0.215**†
Scenario 2	56	0.478*	0.393	-0.212**†
Scenario 3	53	0.408*	0.343	-0.209**†
Scenario 4	133	-0.111	0.009	0.028
Scenario 5	135	-0.103	0.018	0.124
Scenario 6	132	-0.178	-0.040	0.081
Degrees of Freedom	-	23	23	195
$r_{0.05\ 2}$	-	0.396	0.396	0.142
$r_{0.01\ 2}$	-	0.505	0.505	0.185

\* = significant ( $P = 0.05$ ) correlation

† = significant ( $P = 0.01$ ) correlation

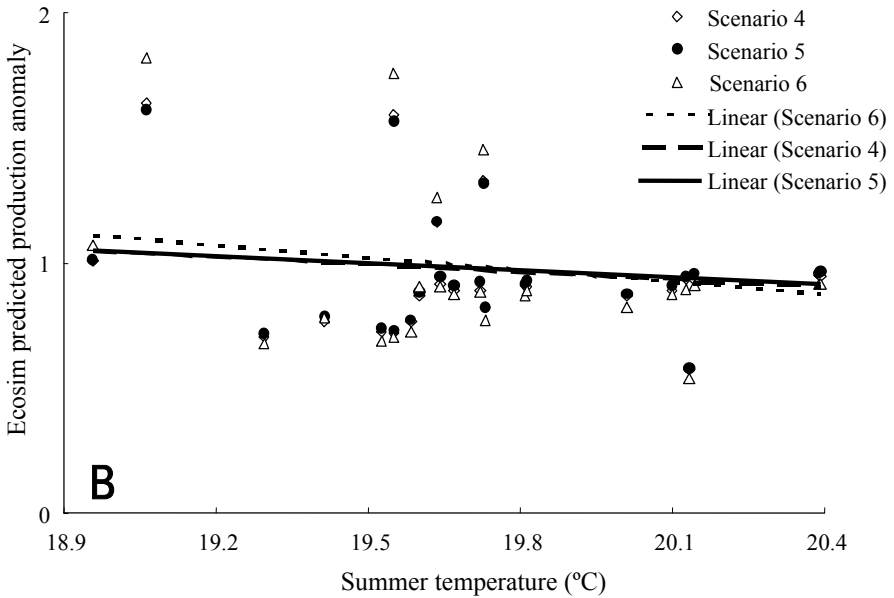
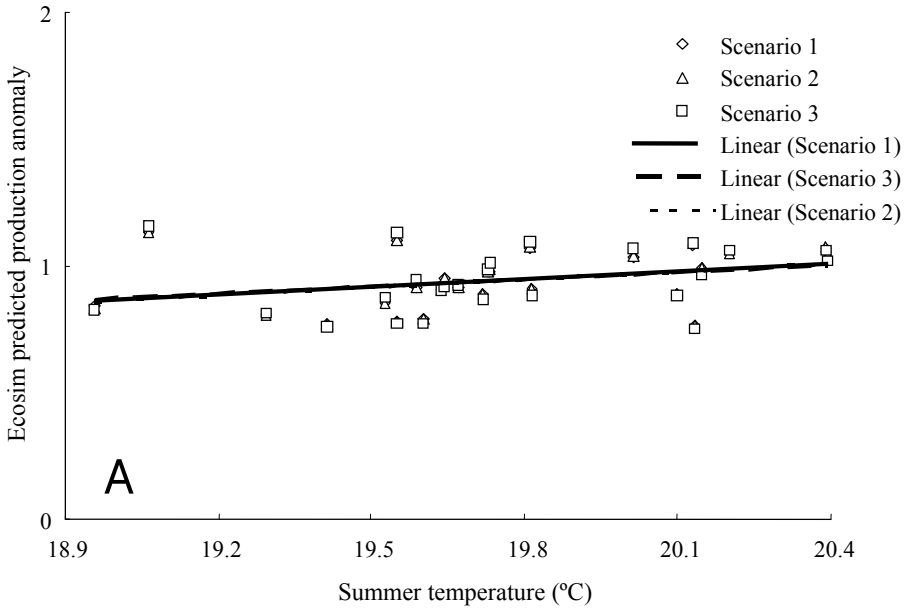


Figure 10. Correlations between three-year average summer sea surface temperature (°C) and the three-year average Ecosim predicted production anomalies for Scenarios 1-3 (Figure 10A) and 4-6 (Figure 10B).



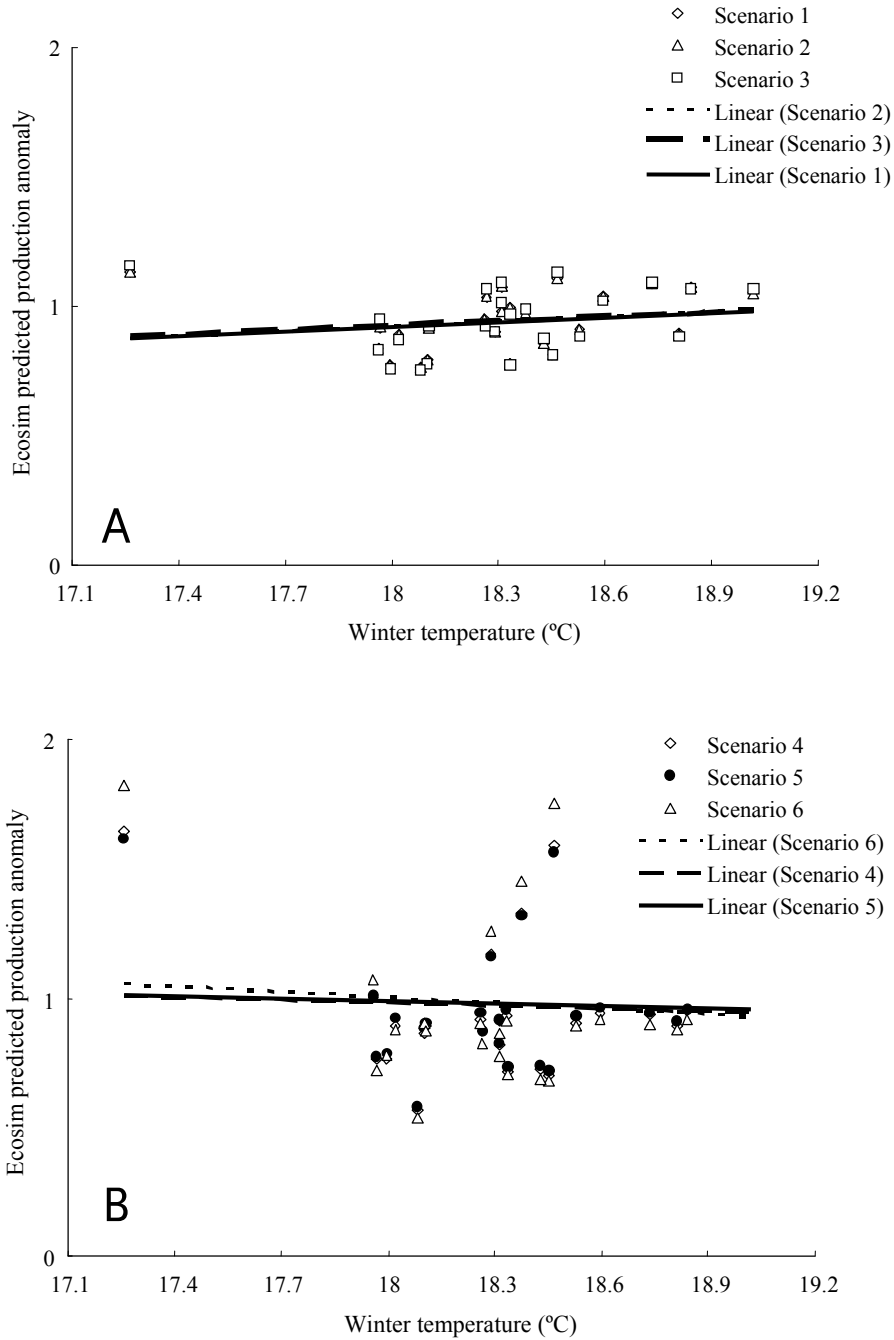


Figure 11. Correlations between the three-year average winter sea surface temperature (°C) and the three-year average Ecosim predicted production anomalies for Scenarios 1-3 (Figure 11A) and 4-6 (Figure 11B).

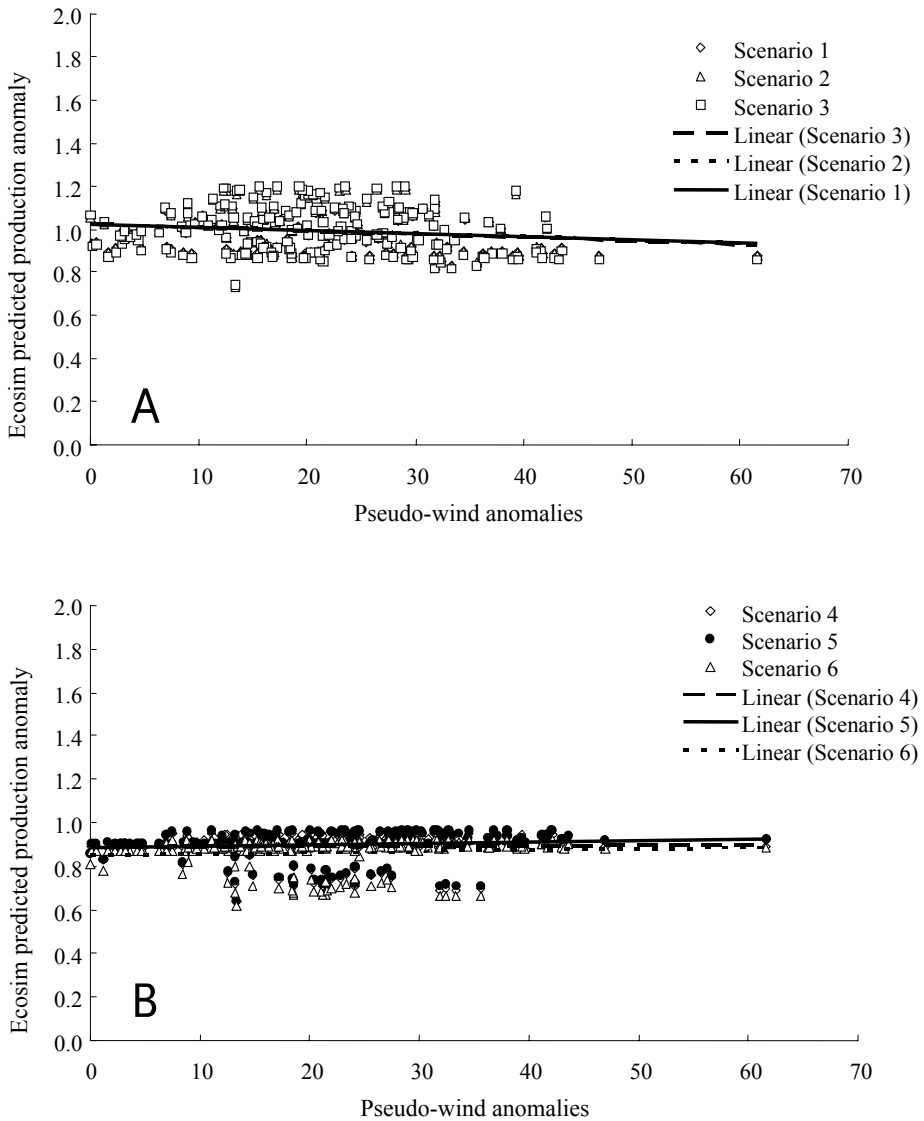


Figure 12. Correlations between the three-year average pseudo wind stress and the three-year average Ecosim predicted production anomalies for Scenarios 1-3 (Figure 12A) and 4-6 (Figure 12B).

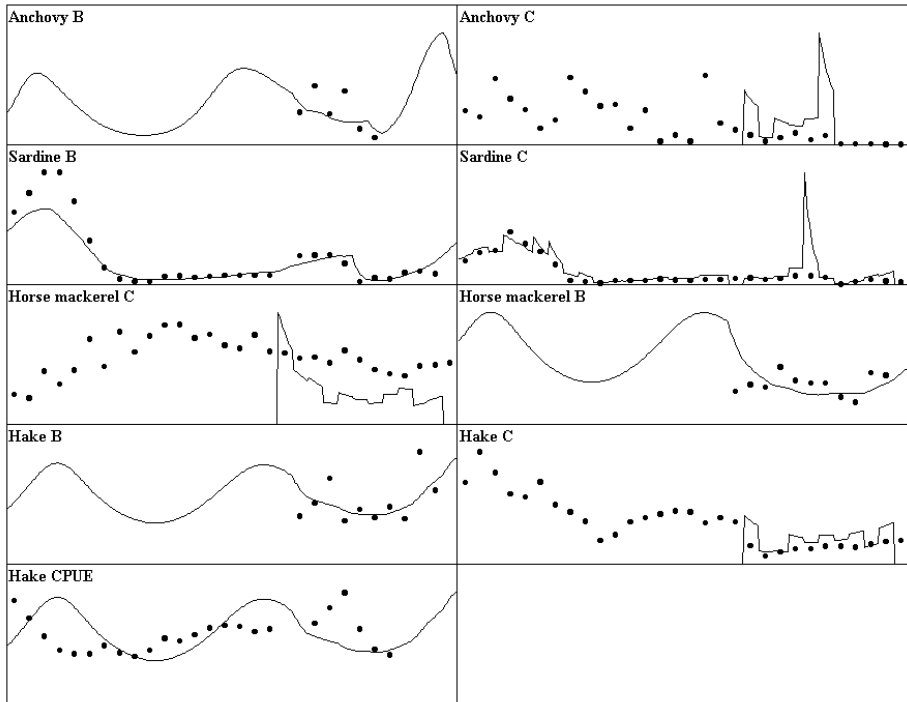


Figure 13. Best run of the 1971-1977 model with time series data incorporated ( $SS = 56$ ). The x-axis represents the time series modelled (1971-2000) and the y-axis shows the relative change in the measured parameter, with C being catch, B being biomass and CPUE being catch per unit effort.

## DISCUSSION AND CONCLUSIONS

The world's fisheries have been massively exploited since the industrialisation of the fishing fleets (Watson and Pauly, 2001). This exploitation has had a devastating effect on the important predatory fish species (Myers and Worm, 2003) and the food web as a whole (Christensen *et al.*, 2003; Jackson *et al.* 2001; Pauly and Palomares, 2001). Similarly, in the southern Benguela ecosystem, fishing over the past 50 years has caused the previously important forage fish species such as anchovy and sardine to collapse (Cury *et al.*, 2000) and fishing over the past 40 years in the northern Benguela ecosystem caused the collapse of the sardine and anchovy populations while the catches of hake and horse mackerel have declined (Boyer and Hampton, 2001).

According to Shannon *et al.* (2000) and Cury *et al.* (2000), modelling the heavy fishing pressure on small pelagic fish in the southern Benguela ecosystem caused stocks of anchovy and sardine to collapse and favoured groups such as chub mackerel and horse mackerel, which compete for zooplankton

prey. In contrast, Shannon and Jarre-Teichmann (1999) showed that a simulated four-fold increase in fishing pressure on small pelagics (anchovy, sardine and gobies) in the northern Benguela system did not show the same increase in chub mackerel and horse mackerel as was seen in the southern Benguela. The reason for the difference is not well understood, but could be due to the higher fishing pressure on horse and chub mackerel in the northern Benguela. The niche vacated by anchovy, sardine and gobies in their simulations of the northern Benguela was probably filled by other small pelagics, rather than by chub and horse mackerel. Shannon *et al.* (2000) showed that the increase in biomass of these competitors in the southern Benguela delayed the recovery of anchovy and sardine since the alleviation of heavy fishing and it took populations longer to recover when “wasp-waist” control was assumed than under bottom-up control. The effect of “wasp-waist” control in the northern Benguela system has not been tested before, but is done here.

The external effects of fishing on the northern Benguela ecosystem since 1970, combined with the internal effects of “wasp-waist” control, reduced the sums of squares of the four groups for which data were available to nearly 50% the sum of squares with fishing alone (Table 1). When estimates of primary production anomalies were obtained from Ecosim using “wasp-waist” control and including the harvest rates of the four groups, the sum of squares was reduced by 65% (Table 1), while the primary production anomalies without “wasp-waist” control only reduced the sum of squares marginally.

The primary production anomalies correlated significantly with summer sea surface temperature (Figures 10 and 11) and pseudo-wind anomalies (Figure 12), the two environmental variables postulated to influence the ecosystem by Cole (1999); Kreiner *et al.* (2000) and Reid *et al.* (2000). These anomalies correlated best with summer sea surface temperature when including a forcing function on both phytoplankton and macrophytes, while the pseudo-wind stress anomalies correlated best with a forcing function on phytoplankton only. The positive correlation between summer sea surface temperature and the forcing functions that included “wasp-waist” control were significant at  $P = 0.05$ , while the negative correlation between pseudo wind stress anomalies and the forcing functions that included “wasp-waist” control were significant to  $P = 0.01$  (Table 1).

The environmental variable that, as a result, seems to have the most significant effect is wind stress, which Kreiner *et al.* (2000) suggested to be a good predictor of sardine spawner biomass and recruitment. The effect of wind on upwelling in general is well known and has been studied extensively by Shannon *et al.* (1990); Andrews and Hutchings (1980) and Nelson and

Hutchings (1983), while Stenevik *et al.* (2001) and Kreiner *et al.* (2000) showed that wind has a significant effect on sardine in particular.

On the other hand, summer sea surface temperature also seems to play an important role in the ecosystem. Sea surface temperature, however, is also related to wind stress, as upwelling is driven by wind and by definition affects sea surface temperature. Thus, it would seem that using wind stress anomalies for future predictions would be more sensible.

Finally, including the internal forcing of forage fish as “wasp-waist” control as well as that of external forcing of pseudo-wind stress and/or summer sea surface temperature explains more of the variability in the ecosystem than any of these variables alone. The resulting estimated biomasses fits best to the biomass time series available (Figure 13) and indicates that both internal and external forces are at work in the northern Benguela ecosystem.

## REFERENCES

- Allen, R.R. (1971): Relation between production and biomass. *Journal of the Fisheries Research Board of Canada* 28: 1573–1581.
- Andrews, W.R.H., and Hutchings, L. (1980): Upwelling in the southern Benguela current. *Proceedings in Oceanography* 9: 1-81.
- Boyer, D.C., Boyer, H.J., Fossen, I., and Kreiner, A. (2001): Changes in abundance of the northern Benguela sardine stock during the decade 1990-2000, with comments on the relative importance of fishing and the environment. *South African Journal of marine Science (A Decade of Namibian Fisheries Science)* 23: 67-84.
- Boyer, D.C., Cole, J., and Bartholomae, C. (2000): Southwestern Africa: Northern Benguela Current Region. *Marine Pollution Bulletin* 41(1-6): 123-140.
- Boyer, D.C., and Hampton, I. (2001): An overview of the living marine resources of Namibia. *South African Journal of Marine Science (A Decade of Namibian Fisheries Science)* 23: 5-35.
- Brown, P.C., Painting, S.J., and Cochrane, K.L. (1991): Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. *South African Journal of Marine Science* 11: 537-564.
- Burmeister, L.-M. (2001): Depth-stratified density estimates and distribution of the Cape hake *Merluccius capensis* and *M. paradoxus* off Namibia deduced from survey data, 1990-1999. *South African Journal of Marine Science (A Decade of Namibian Fisheries Science)* 23: 347-356.
- Butterworth, D.S., and Geromont, H.F. (2001): Evaluation of a class of possible simple interim management procedures for the Namibian hake fishery. *South African Journal of Marine Science (A Decade of Namibian Fisheries Science)* 23: 357-374.
- Christensen, V., Guénette, S., Heymans, J. J., Walters, C., Watson, R., Zeller, D., and Pauly, D. (2003): Hundred-year decline of North Atlantic predatory fishes. *Fish and Fisheries* 4: 1-24.
- Christensen, V. and Walters, C.J. (2004):

- Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* 172: 109-139.
- Christensen, V., Walters, C., and Pauly, D. (2000): *Ecopath with Ecosim: A User's guide*. Fisheries Centre, University of British Columbia and ICLARM, Vancouver, BC and Penang, Malaysia, 131 pp.
- Cole, J. (1999): Environmental conditions, satellite imagery, and clupeoid recruitment in the northern Benguela upwelling system. *Fisheries Oceanography* 8(1): 25-38.
- Cole, J., and Villacastin, C. (2000): Sea surface temperature in the northern Benguela upwelling system, and implications for fisheries research. *International Journal of Remote Sensing* 21(8): 1597-1617.
- Cram, D.L. (1981): Hidden elements in the development and implementation of marine resource conservation policy: the case of the South West African/Namibian fisheries. In: *Resource Management and Environmental Uncertainty: Lessons from Coastal Upwelling Fisheries*. M.H. Glantz and J.D. Thompson (Eds.). New York, Wiley: 137-155.
- Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, A., Shannon, L.J., and Verheye, H. M. (2000): Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES Journal of Marine Science* 57: 603-618.
- Estrada, M., and Marrase, C. (1987): Phytoplankton biomass and productivity off the Namibian coast. *South African Journal of Marine Science* 5: 347-356.
- Fossen, I., Boyer, D.C., and Plarre, H. (2001): Changes in some key biological parameters of the northern Benguela sardine stock. *South African Journal of Marine Science* (A Decade of Namibian Fisheries Science) 23: 111-121.
- Heymans, J.J. (1997): Network Analysis of the Carbon Flow Model of the northern Benguela Ecosystem, Namibia. Ph.D. Thesis. Zoology Department, University of Port Elizabeth, 206 pp.
- Heymans, J.J. and Baird, D. (2000): Network analysis of the northern Benguela ecosystem by means of NETWRK and Ecopath. *Ecological Modelling* 131: 97-119.
- Heymans, J.J., Shannon, L.J. and Jarre, A. (2004): Changes in the northern Benguela ecosystem over three decades: 1970s, 1980s and 1990s. *Ecological Modelling* 172(2-4): 175-195.
- Jackson, J.B.C., Kirby M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R. (2001): "Historical Overfishing and the Recent Collapse of Coastal Ecosystems." *Science* 293: 629-638.
- Jarre-Teichmann, A. (1998): The potential role of mass-balance models for the management of upwelling ecosystems. *Ecological Applications* 8 (1) Sup.: 93-103.
- Jarre-Teichmann, A. and Christensen, V. (1998): Comparative modelling of trophic flows in four large upwelling ecosystems: global vs. local effects. In: Durant, M.H., Cury, R., Mendelssohn, R., Roy, C., Bakun, A. and Pauly, D. (Eds.). *From Local to Global Changes in Upwelling Systems*, pp. 423-443. ORSTROM, Paris.
- Kreiner, A., Mouton, D., Daskalov, G., Clement, A. and Wiggert, J. (2000): Namibian sardine fisheries and its interaction with environmental conditions. Presentation given at the

- Workshop on Interannual Climate Variability and Pelagic Fisheries, Nouméa, Nouvelle Calédonie, 6th - 24th November 2000.
- Lutjeharms, J.R.E., and Meeuwis, J.M. (1987): The extent and variability of South-East Atlantic upwelling. *South African Journal of Marine Science* 5: 51-62.
- Mendelsohn, R. and Roy, C. (1996): Comprehensive Ocean Data Extraction Users Guide. U.S. Dep. Comm. NOAA Tech. Memo. NOAA-TM-NMFS.SWFSC-228, La Jolla, California. 67 pp.
- Myers, R.A., and Worm, B. (2003): Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280-283.
- Nelson, G., and Hutchings, L. (1983): The Benguela upwelling area. *Proceedings in Oceanography* 12(3): 333-356.
- Pauly, D., and Palomares, M.L.D. (2001): Fishing down marine food web: it is far more pervasive than we thought. In: Conference on Sustainability of Fisheries Rosenstiel School of Marine Sciences, University of Miami, 26-28 November, 2001.
- Reid, P.C., Battle, E.J.V., Batten, S.D. and Brander, K.M. (2000): Impacts of fisheries on plankton community structure. *ICES Journal of Marine Science* 57: 495-502.
- Shackleton, L.Y. (1987): A comparative study of fossil fish scales from three upwelling regions. *South African Journal of Marine Science* 5: 79-84.
- Shannon, L.J. and Crawford, R.J.M. (2003): Report of the SPACC/BENEFIT/IDYLE working group on major turning points in the Benguela ecosystem during the latter half of the 20th century Cape Town, February 2001.
- Shannon, L.J., and Jarre-Teichmann, A. (1999): Comparing models of trophic flows in the Northern and Southern Benguela Upwelling systems during the 1980s. In: *Ecosystem Considerations in Fisheries Management*, pp. 527-541, Anchorage, Alaska, Alaska Sea Grant College Program. AK-SG-99-01.
- Shannon, L.J., Cury, P. and Jarre, A. (2000): Modelling effects of fishing in the Southern Benguela ecosystem. *ICES Journal of Marine Science* 57: 720-722.
- Shannon, L.V., Agenbag, J.J. and Buys, M.E.L. (1987): Large- and mesoscale features of the Angola-Benguela front. *South African Journal of Marine Science* 5: 11-34.
- Shannon, L.V., Lutjeharms, J.R.E., and Nelson, G. (1990): Causative mechanisms for intra-annual and interannual variability in the marine environment around Southern Africa. *South African Journal of Science* 86: 356-373.
- Stenevik, E.K., Sundby, S. and Cloete, R. (2001): Influence of buoyancy and vertical distribution of sardine *Sardinops sagax* eggs and larvae on their transport in the northern Benguela ecosystem. *South African Journal of Marine Science (A Decade of Namibian Fisheries Science)* 23: 85-97.
- Thomas, R.M. (1986): The Namibian pilchard: the 1985 season, assessment for 1952-1985 and recommendations for 1986. *Collection of Scientific Papers of the International Commission of South East Atlantic Fisheries* 13(2): 243-269.
- Vaske, B. and Klingelhoeffer, E. (2001): Review of stock assessment for Cape horse mackerel off Namibia. Paper prepared for the Horse mackerel Workshop, 26-29 March 2001, MFMR, Swakopmund, Namibia.
- Walters, C., Christensen, V., and Pauly, D. (1997): Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Re-*

- views in Fish Biology and Fisheries* 7: 139-172.
- Walters, C., Pauly, D., Christensen, V., and Kitchell, J. F. (2000): Representing Density Dependent Consequences of Life History Strategies in Aquatic Ecosystems: EcoSim II. *Ecosystems* 3: 70-83.
- Watson, R., and Pauly, D. (2001): Systematic distortions in world fisheries catch trends. *Nature* 414: 534-536.
- Willemse, N.E. (2002): Major trends in the marine fisheries catches off Namibia, 1950-2000. Department of Biology, Norwegian College of Fishery Science, University of Tromsø, Norway, 65 pp.
- Willemse, N. and Pauly, D. (2004): Re-construction and interpretation of marine fisheries catches from Namibian waters, 1950 to 2000. In *Namibia's fisheries: Ecological, economic and social aspects*, Sumaila, U.R., Boyer, D., Skogen, M. and Steinshamn, S.I. (eds.), pp. 99-112. Eburon, Delft.
- Winberg, G.G. (1956): Rate of metabolism and food requirements of fishes. *Translations of the Fisheries Research Board of Canada* 194: 1-253.
- Woodruff, S.D., Slutz, R.J., Jenne, R.L. and Steurer, P.M. (1987): A Comprehensive Ocean Atmosphere Data-Set. *Bulletin of the American Meteorological Society* 68: 1239-1250.